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Effect of Different Photon Flux Densities (PAR) on Seedling Growth and Morphology of *Metrosideros collina* (Forst.) Gray[1]

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ABSTRACT: Seedlings of *Metrosideros* were capable of net accumulation of dry matter at photon flux densities as low as 13 μmol m^{-2} s^{-1} PAR (about 0.6 percent sunlight), when grown under a 12-hour daylength at 20° or 25°C for over 4 months. Seedlings became adapted to shade at low levels of PAR by an increased leafiness of the plant (expressed as the leaf area ratio). This increased leafiness was brought about by a marked reduction in leaf thickness rather than by an increase in the proportion of assimilates distributed to leaves.

'ŌHI'A (*Metrosideros* sp., Myrtaceae) AND KOA (*Acacia Koa* Gray) are the two major endemic tall trees found in the Hawaiian rain forests. *Metrosideros collina* (Forst.) Gray is a highly variable species, with seedlings capable of colonizing the high-radiation environment of a lava flow exposed to full sunlight or the highly shaded environment of a tree-fern stem (*Cibotium* sp.) deep within the rain forest (Corn 1972, Smathers and Mueller-Dombois 1974). As part of studies on the importance of radiation in controlling the regeneration of *Metrosideros* in the forest environment, the following experiments were carried out to determine the lower limit of photosynthetically active radiation (PAR) over the wavelength range 400 to 700 nm needed to support early growth of seedlings. The methods of growth analysis (reviewed by Květ et al. 1971) were used to further examine the adaptive response of seedlings to the level of PAR at which they were grown.

MATERIALS AND METHODS

Mature seed of *Metrosideros collina* (Forst.) Gray subsp. *polymorpha* (Gaud.) Rock was obtained from the Kilauea rain forest on the island of Hawaii. All seed was from one seed cluster, and was sown on the surface of pieces of shredded hāpu'u (tree-fern root) in 4-inch plastic pots. The pots were watered from below and the tops of the pots were covered with plastic Petri dish lids.

Germination took place in about one week in a growth room maintained at a constant temperature of 25°C and a daylength of 12 hours provided by white fluorescent lamps. The photon flux density of wavelengths in the photosynthetically active part of the spectrum from 400 to 700 nm (PAR level) was measured with a Lambda Instruments quantum sensor LI-185. For white fluorescent lamps, 1 μmol $m^{-2}s^{-1}$ PAR was equivalent to 48 lux. Seeds were germinated at PAR values of 40 μmol $m^{-2}s^{-1}$ and then transferred to a series of PAR levels ranging from 8 to 235 μmol $m^{-2}s^{-1}$ in growth rooms maintained at a 12-hour daylength at either 20° or 25°C. A second series of plants was transferred to a similar series of PAR levels but under a 24-hour daylength at 20°C. The different levels of PAR were obtained by varying the distance of the plants from the light.

Plants were watered with one-quarter strength Hoaglands solution (Hoagland and Arnon 1939), at 2- to 3-day intervals, and harvested after 126 days growth at the 12-hour daylength and after 262 days at the 24-hour daylength. The number of leaves and

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total plant dry weights were measured for plants grown under 12-hour daylengths. In addition, the number of nodes and leaf, stem, and root weights were recorded for the 24-hour series. Six replicate pots of 3 to 5 plants were grown at each different treatment combination of temperature and PAR level, giving mean values for growth measurements based on 20 to 30 replicate plants per treatment.

Measurements of leaf area were taken for plants grown in the 24-hour daylength so that some of the methods of growth analysis could be used to determine the nature of the adaptive response to shading. Leaves were flattened by a glass plate and photoduplicated in a dry copy machine, and leaf areas were determined by cutting out the leaf outlines, weighing the paper, and calculating the leaf area from the known area per unit weight of paper. Measurements of leaf area (A) and total plant dry weight (W) were used to calculate the leaf area ratio (AW^{-1}, dm^2g^{-1}) a measure of "leafiness." This ratio is the product of two other ratios, one morphological, an assessment of leaf thickness, and the other physiological, a measure of the way in which assimilates are distributed to developing leaves, stem, or root. The assessment of leaf thickness is given by the specific leaf area, AW_L^{-1}, dm^2g^{-1}, the ratio of leaf area to leaf dry weight—the higher the ratio the thinner the leaf. This relationship has recently been confirmed for *Metrosideros* (Corn 1979). A measure of assimilate distribution to the leaves is given by the leaf weight ratio, the ratio of the dry weight of leaves to that of the whole plant (W_LW^{-1}). The relationship between the leaf area ratio and its two components is $AW^{-1} = AW_L^{-1}\ (W_LW^{-1})$. The ratios of the dry weights of stems (W_S) and roots (W_R) to that of the whole plant (W_SW^{-1} and W_RW^{-1}) similarly measure the distribution of assimilates to plant parts other than leaves. These three ratios provide more precise information on the nature of assimilate partitioning than the shoot/root ratio, $(W_S + W_L)\ W_R^{-1}$. The other components of growth analysis, the relative growth rate and net assimilation rate, were not measured in these experiments.

RESULTS

At both 24- and 12-hour daylengths, seedlings survived at the lowest PAR values used (8 to 13 μmol $m^{-2}s^{-1}$), a level about 0.6 percent that of full sunlight. Plants were actually accumulating carbon at this PAR level as the mean total plant dry weight was over 0.1 mg even at the lowest PAR level used at 25°C; this plant dry weight was greater than the dry weight of the very small seed (about 0.07 mg per seed). With increased PAR levels at both daylengths, total plant dry weight, number of leaves, and number of nodes increased (Figures 1, 2, and 3).

The nature of the growth response to PAR level was analyzed more fully for the 24-hour daylength series. Plants became morphologically modified at low PAR values by a reduction in leaf thickness, as measured by the increased specific leaf area (AW_L^{-1} in Figure 4). The PAR level had less effect on the proportion of assimilates distributed to leaves, measured as the leaf weight ratio (W_LW^{-1} in Figure 4) which was lowest at low PAR values. Because of the large effect of PAR on AW_L^{-1} the net result was an increased "leafiness" at low PAR levels, "leafiness" being measured as the leaf area ratio (AW^{-1} in Figure 4). The proportion of roots was little affected by PAR level (W_RW^{-1} in Figure 5), so that the decreased W_LW^{-1} at low PAR levels was mainly attributable to the increased diversion of assimilates into stem (increased W_SW^{-1} in Figure 5).

DISCUSSION

The ability of seedlings of *Metrosideros* to grow at PAR levels as low as 0.6 percent sunlight was achieved mainly by the adaptive changes that occurred in leaf thickness (increase in AW_L^{-1} with decreasing PAR levels in Figure 4). This photomorphogenetic effect was a direct consequence of the altered level of PAR. The ratio of energies in the red and far-red regions of the spectrum was maintained constant, unlike the field situation where shading by leaves of other plants lowers the ratio of energy at 600 nm (red) to

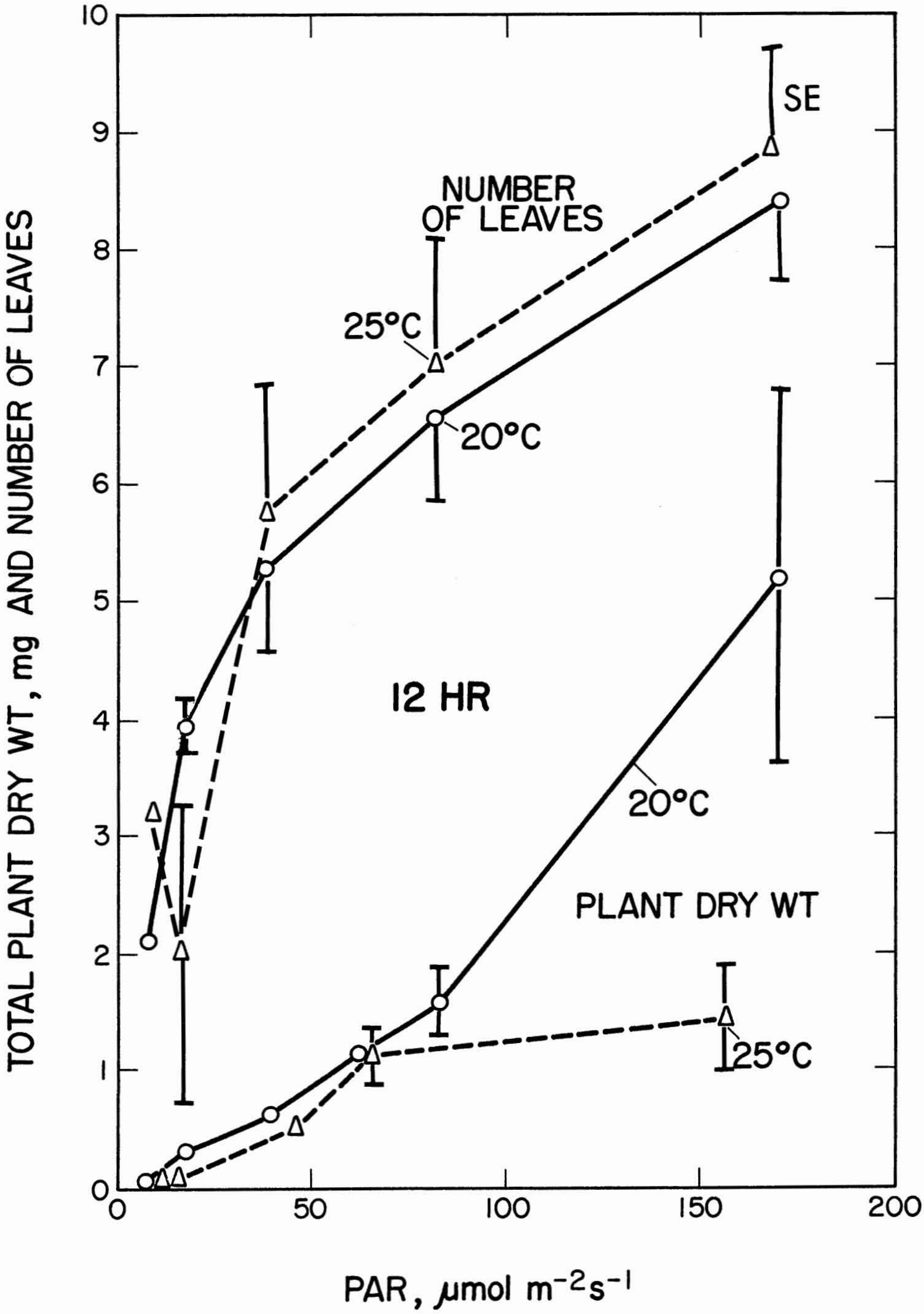

FIGURE 1. Effect of PAR level during growth on leaf number and total plant dry weight of *Metrosideros* seedlings grown for 126 days under a 12-hour daylength at either 20° or 25°C constant temperature. Points are mean values from about 30 plants.

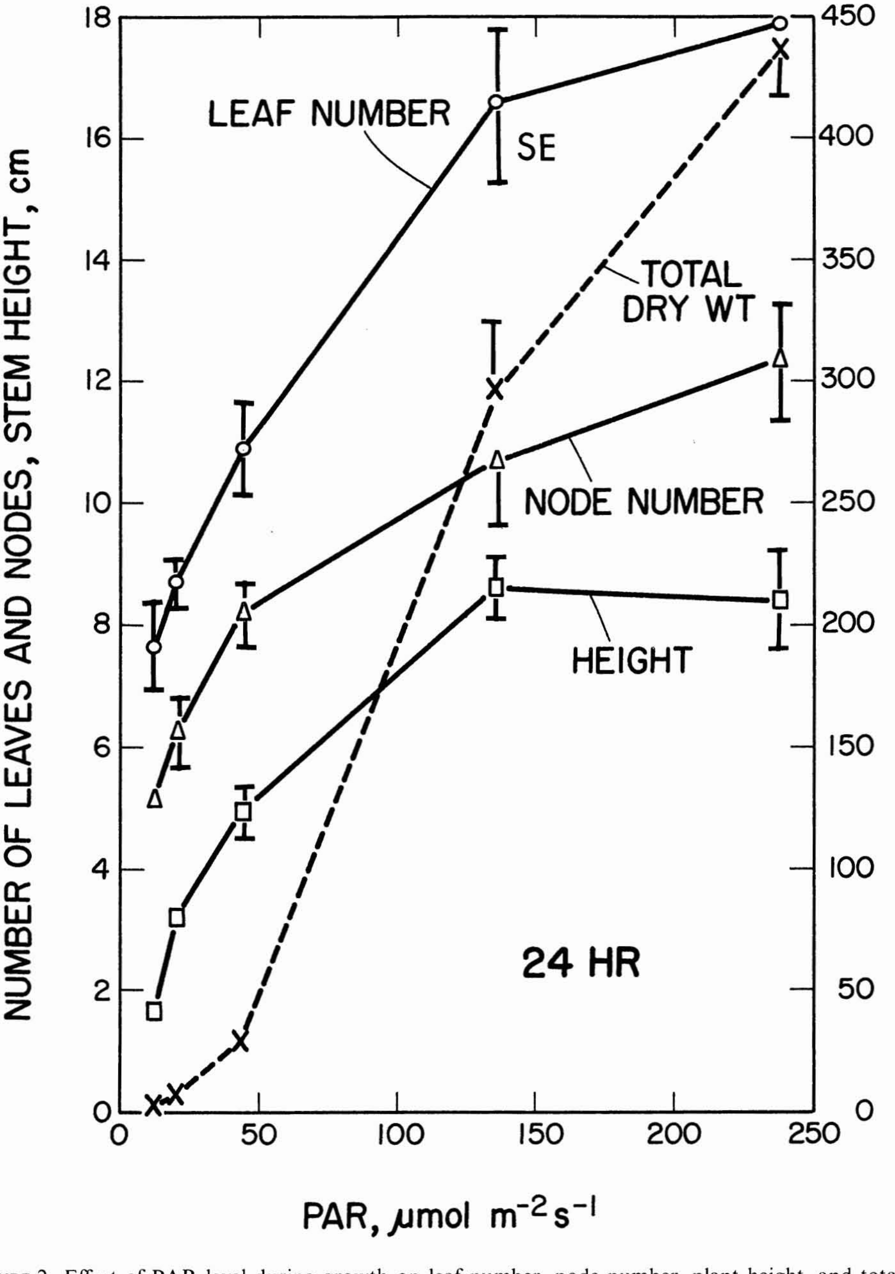

FIGURE 2. Effect of PAR level during growth on leaf number, node number, plant height, and total plant dry weight of *Metrosideros* seedlings grown for 126 days under a 24-hour daylength at 20°C. Points are mean values from about 30 plants.

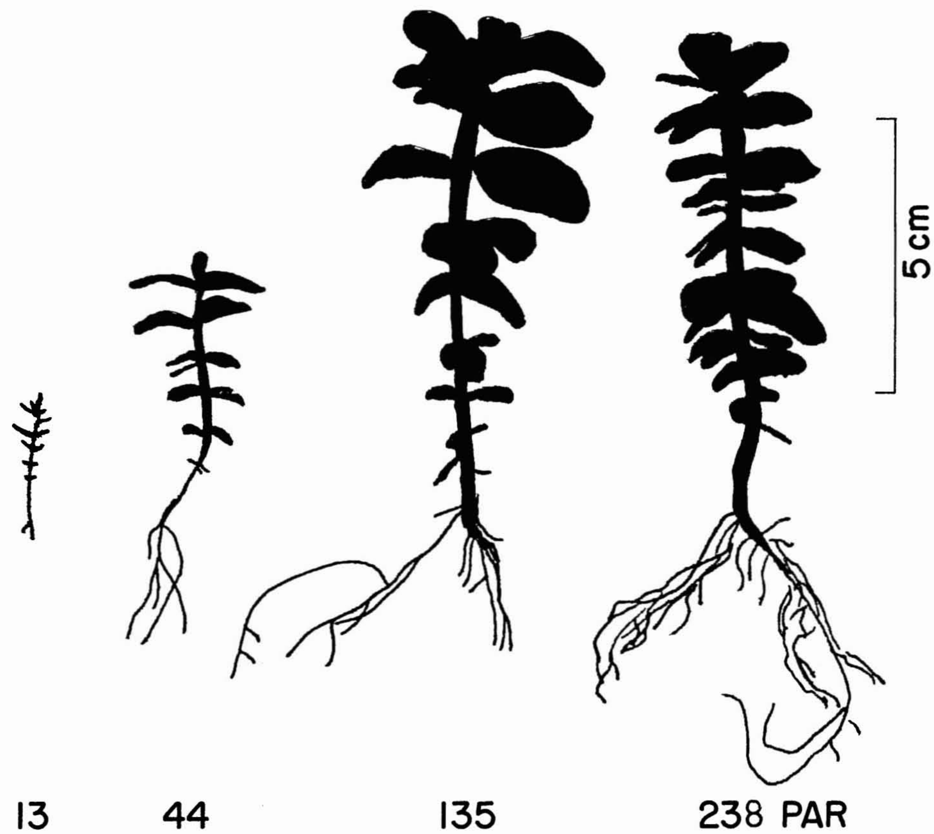

FIGURE 3. Morphology of *Metrosideros* seedlings grown for 262 days under a 24-hour daylength at 20°C at PAR values of 13, 44, 135, and 235 μmol m^{-2} s^{-1}.

that at 730 nm (far red), with profound consequences on the action of the photomorphogenetic pigment phytochrome (Holmes and McCartney 1976).

Leaf thickness increases from the earliest- to the later-formed leaves in seedlings of *Metrosideros*, so that the increased leafiness of plants grown at low levels of PAR may be in part a result of their more juvenile stage of development. Such ontogenetic changes are well documented in other plants (e.g., Friend, Helson, and Fisher 1962).

Another morphological consequence of low levels of PAR was the increased proportion of assimilates distributed to stems, shown by the increase in $W_S W^{-1}$ (Figure 5). The length of stem for each unit dry weight of stem was also increased under shade. Values of stem height per milligram were 1.7, 2.3, 7.4, 16.6, and 23.6 cm over the range of PAR values of 235, 135, 44, 21, and 13 μmol $m^{-2}s^{-1}$ respectively. Both these adaptations (etiolation) would optimize photon capture in photosynthesis by carrying the leaves above the shade of competing seedlings. As in the case of leaf adaptations, ontogenetic changes in stem morphology cannot be separated from direct effects of the environment in these studies.

The PAR level necessary for early seedling growth of *Metrosideros* seedlings with adequate mineral and water supply is probably close to 10 μmol $m^{-2}s^{-1}$ under a 12-hour daylength at 20°C (Figure 1). The lower limits of PAR level are at present not known for successful establishment of *Metrosideros* seedlings within the deep shade of the rain forest. However, an examination of the size

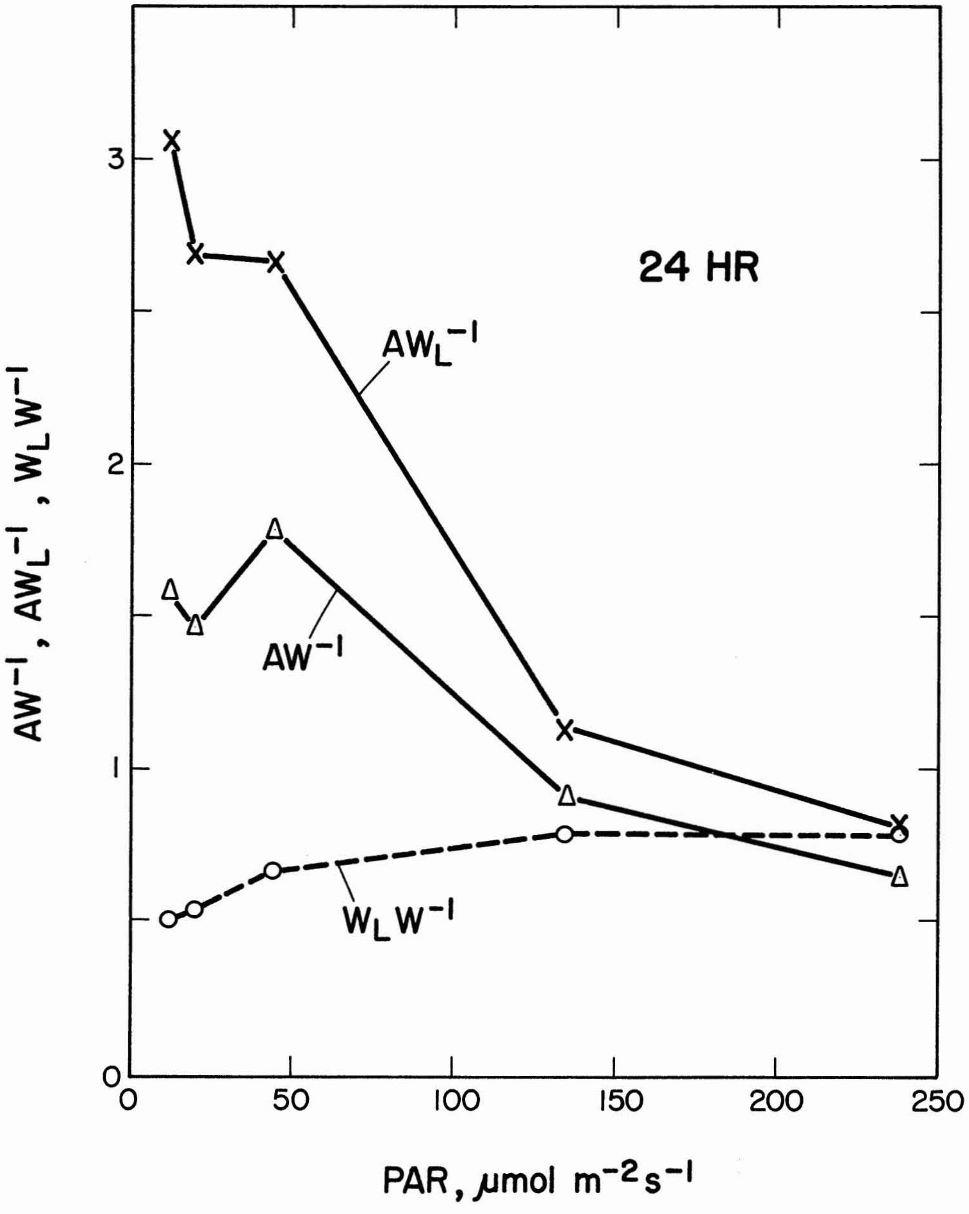

FIGURE 4. Effect of PAR level on the leaf area ratio (AW^{-1}) and its two components, the leaf weight ratio ($W_L W^{-1}$) and the specific leaf area (AW_L^{-1}). Seedlings of *Metrosideros* grown at 20°C under a 24-hour daylength for 262 days. Points are mean values from 20 plants.

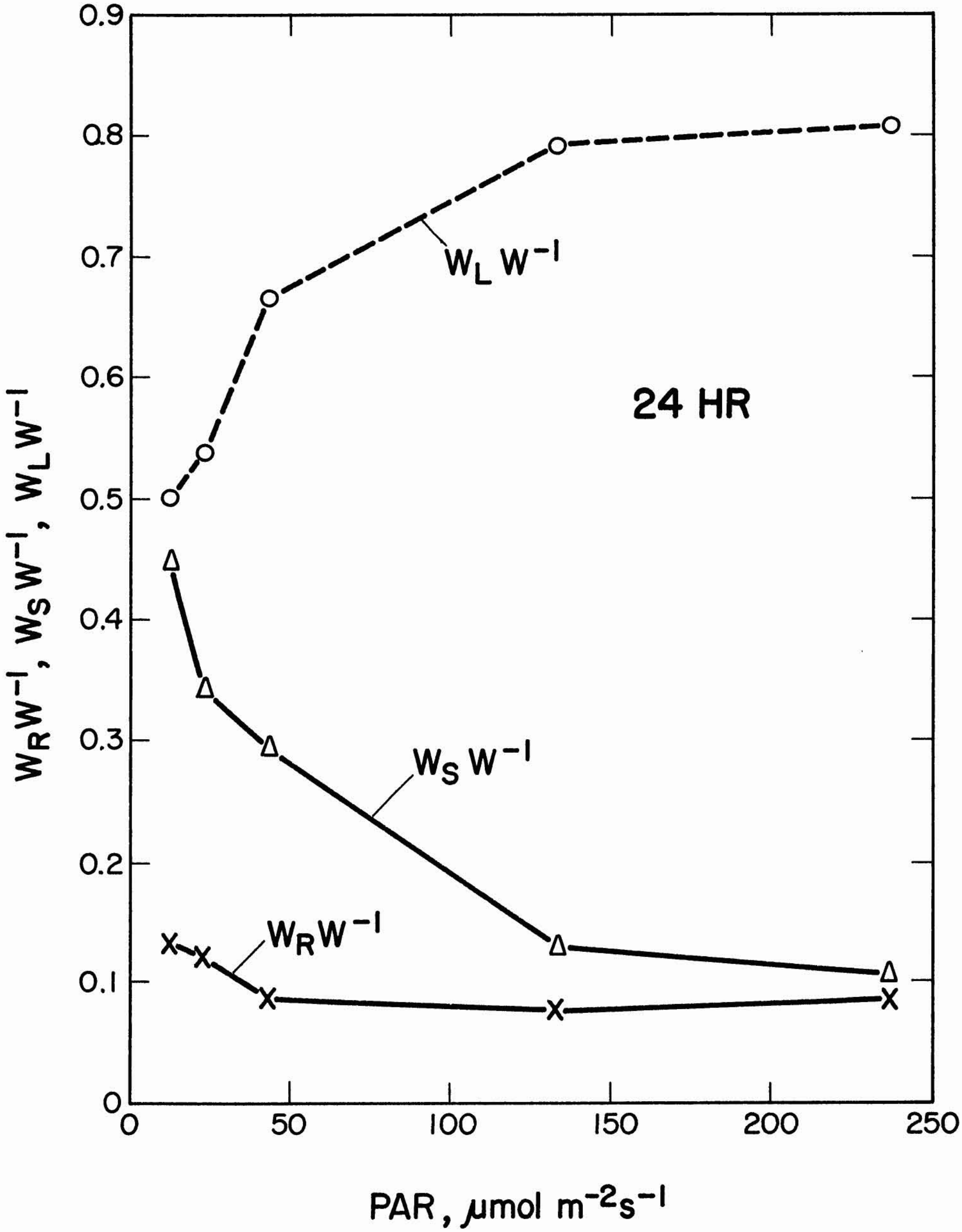

FIGURE 5. Effect of PAR level on the distribution of assimilates to leaves ($W_L W^{-1}$), stems ($W_S W^{-1}$) and roots ($W_R W^{-1}$). Seedlings of *Metrosideros* grown at 20°C under a 24-hour daylength for 262 days. Points are mean values from 20 plants.

classes present in young plants of *Metrosideros* in a healthy rain forest showed about 104 plants per hectare less than 10 cm in height but only 10 between 50 and 100 cm and none between 1 and 5 m (Mueller-Dombois 1977). A similar rapid decline in densities between size classes below and above 50 cm was found by Cooray (1974). Further work is necessary to determine the lowest PAR level at which long-term seedling establishment can succeed and the physiologically basis of shade tolerance in young trees.

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LITERATURE CITED

COORAY, R. G. 1974. Stand structure of a montane rain forest on Mauna Loa, Hawaii. M.S. Thesis. University of Hawaii, Honolulu. x + 167 pp.

CORN, C. A. 1972. Seed dispersal methods in Hawaiian *Metrosideros*. Pages 442–435 *in* J. A. Behnke, ed. Challenging biological problems: directions toward their solution. Oxford University Press, New York.

———. 1979. Variation in Hawaiian *Metrosideros*. Ph.D. Thesis. University of Hawaii, Honolulu. xvi + 295 pp.

FRIEND, D. J. C., V. A. HELSON, and J. E. FISHER. 1962. Leaf growth in Marquis wheat, as regulated by temperature, light intensity, and daylength. Can. J. Bot. 40:1299–1311.

HOAGLAND, D. R., and D. I. ARNON. 1939. The water culture method for growing plants without soil. Circ. Calif. Agric. Exp. Stn. 347:1–39.

HOLMES, M. G., and H. A. MCCARTNEY. 1976. Spectral energy distribution in the natural environment and its implications for phytochrome function. Pages 467–476 *in* H. Smith, ed. Light and plant development. Butterworths, London.

KVĚT, J., J. P. ONDOK, J. NEČAS, and P. G. JARVIS. 1971. Methods of growth analysis. Pages 343–391 *in* Z. Šesták, J. Čatský, and P. G. Jarvis, eds. Plant photosynthetic production. Manual of methods. Dr. W. Junk, The Hague. xxxii + 800 pp.

MUELLER-DOMBOIS, D. 1977. Ohia rainforest study. Tech. Rep. 20. CPSU/UH 010/6. Botany Dept. University of Hawaii, Honolulu. 117 pp.

SMATHERS, G. A., and D. MUELLER-DOMBOIS. 1974. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. National Park Service Sci. Man. Ser. 5. Pub. No. NPS 118. 129 pp.